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Background complexity and the detectability of camouflaged targets by birds and humans

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Abstract

Remaining undetected is often key to survival, and camouflage is a widespread solution. However, extrinsic to the animal itself, the complexity of the background may be important. This has been shown in lab experiments using artificially patterned prey and backgrounds, but the mechanism remains obscure (not least because 'complexity' is a multifaceted concept). In this study, we determined the best predictors of detection by wild birds and human participants searching for the same cryptic targets on trees in the field. We compared detection success to metrics of background complexity and 'visual clutter' adapted from the human visual salience literature. For both birds and humans, the factor that explained most of the variation in detectability was the textural complexity of the tree bark as measured by a metric of feature congestion (specifically, many nearby edges in the background). For birds, this swamped any effects of colour match to the local surround although, for humans, local luminance disparities between the target and tree became important. For both taxa, a more abstract measure of complexity, entropy, was a poorer predictor. Our results point to the common features of background complexity that affect visual search in birds and humans, and how to quantify them.

Key words: camouflage, background complexity, visual search, clutter metrics

Introduction

Avoiding detection is frequently important, whether for prey avoiding predators, predators approaching prey, males sneaking mating opportunities, or subordinate individuals avoiding harassment by dominants. Camouflage is one of the most widespread adaptations for concealment, although it is perhaps more usefully thought of, not as one process, but as a collection of mechanisms that interfere with detection, recognition and successful attack [1-4].

Various factors have been proposed to affect detectability of an animal: the similarity in colour and pattern between prey and background (the degree of background matching) both in terms of local contrast with the immediate background and coarse-grained similarity to the features of the habitat as a whole [5-9], the coherence of shape and outline (as opposed by disruptive colouration) [10-12]; distraction of attention from salient features [13, 14, but see 15, 16]; salience of distinctive body parts such as eyes [17]; symmetry or repetition of features [18-20]; also, as a factor extrinsic to the prey, the complexity of the background [7]. The latter has been investigated in lab experiments using artificially patterned prey and backgrounds, with birds [14, 21, 22] and fish [23]. There is value in replicating experiments on the effects of background complexity under more natural conditions; natural textures differ from the types of artificial textures used in these experiments in many ways, such as the contrast range and how deterministic or periodic the pattern is [24]. Importantly, although these studies have demonstrated effects of background 'complexity' ("high variability or complexity in shapes of the elements constituting the background" [21]), it is not clear which aspects of complexity interfere with visual search, nor how one could translate this, intuitively reasonable, verbal description

into a numerical measure of complexity. With camouflaged targets and complex natural textures, this is a challenge because the targets (and any objects or features in the background that they are similar to) have not been segmented (visually separated) from the background and the features that might be used to discriminate between target and background are not pre-specified by the experimenter.

In this study, we tested the effect of background complexity on the detection success of wild birds preying on artificial prey on various trees in natural woodland. All prey were identical, allowing us to attribute differences in detection success to features of the background and the relationship between the target and the background. We used prey of a single colour, the mean of the background, because introducing patterning on the prey would greatly increase the number of possible dimensions of difference from the different tree backgrounds. The same experiment was replicated, using the exact same targets in the exact same locations, using human subjects. This allowed us to identify similarities and differences between humans and birds searching for the same targets against the same backgrounds under the same lighting conditions. To our knowledge, this is the first time this has been done. Photographs were taken of all targets with a calibrated digital camera, so that human and avian detection could be related to visual features of the prey and their immediate background *in situ*. These were measures of background complexity, plus species-specific estimates of local colour contrast.

We used two measures of background complexity: entropy, an information theoretic metric popular in signal processing, and feature congestion [25]. The latter, based on the variation in features encoded in the early stages of vision, (luminance, colour,

orientation of edges) has proved successful at predicting interference with human visual search [26], with applications in applied contexts such as detection of warning signals in complex visual displays. Other approaches, for example based on spatial sampling [38] are conceptually similar to feature congestion, but we take the approach based on low level vision. We adapted the model of Rosenholtz et al. [25, 26] for avian colour vision.

Methods and Materials

The experimental design was similar to Cuthill et al. [10]; both human and bird field predation experiments were conducted using the same general techniques described for this and similar experiments, but with a different target colour. Targets were triangular in shape (42 mm wide x 20 mm high) in order to resemble a non-specific Lepidopteran. Only one colour was used (see Supplementary Material), with 130 replicates: the average colour of tree bark taken from calibrated photos of 100 trees in exactly the same area of the woods as the experiment (Leigh Woods National Nature Reserve, North Somerset, UK, 2°38.6'W, 51°27.8'N). The targets were printed so as to match the average bark colour as viewed by a passerine bird, the blue tit (*Cynanistes caeruleus*), as determined by single and double cone photon catches (i.e. photon catch paper = photon catch bark). This and other passerine species have been seen predating the artificial prey in previous experiments. The colour was quantified using spectrophotometry and avian colour space modelling [following 27].

This experiment was conducted from November 2011 to January 2012. For avian predation, a dead mealworm (*Tenebrio molitor* larva, frozen overnight at -80°C, then

106 thawed) was attached underneath the artificial ‘moth wings’, then pinned on a tree
107 with ca. 5 mm protruding. Trees were selected according to constraints important for
108 the human experiment, as follows. All targets had to be in open view of the path,
109 potentially visible from at least 20 m distance but passed no further than 2 m distant,
110 and between 1.5 and 1.8 m height on the tree trunk (about the average eye level of
111 an adult). Not every tree was used, so participants could not guess whether a target
112 was present. Trees were not initially selected for the experiment with respect to
113 species, but five were retrospectively identified as having been used: ash (*Fraxinus*
114 *excelsior*) N=9, beech (*Fagus sylvatica*) N=32, cherry (*Prunus avium*) N=3, oak
115 (*Quercus robur*) N=84, yew (*Taxus baccata*) N=2. With the highly unbalanced and,
116 for some species, low sample sizes, effects of tree species *per se* cannot be
117 determined with great reliability but the analysis did consider possible species effects
118 because they may be confounded with other predictors (e.g. oak bark is markedly
119 more patterned than that of beech). Targets were checked at 24, 48 and 72 h;
120 disappearance of the mealworm was scored as ‘predation’, predation by
121 invertebrates (spiders, ants, slugs) and survival to 72 h were scored as ‘censored’
122 and results were analysed using Cox proportional hazards regression [28]. This is a
123 semi-parametric form of survival analysis that allows analysis of the effects of risk
124 factors on survival; we used the *survival* package [29] in R v.2.14.0 (R Development
125 Core Team 2011).

126

127 In the human detection experiment, run immediately after the bird experiment, the
128 same targets on exactly the same trees were used. The total transect, about 1 km
129 long, took participants from 40 to 60 min to walk. Twenty human participants, none
130 colour blind and all with normal or corrected-to-normal vision, were shown an

example target and instructed to walk slowly along the path, with an experimenter following behind, and to stop when they had detected a target. Participants used a laser range finder (Leica Disto D5; Leica Geosystems GmbH, Munich, Germany) to measure detection distance if the target was detected. The experimenter walked just behind the participant, so as not to influence them, and recorded the distances and any targets missed. Use of the laser rangefinder also dissuaded participants from guessing, as the laser dot confirmed correct target location (there were no false positives in any trials). Human detection was estimated by two response variables: detection (binary) and, if it was detected, the detection distance to the nearest cm.

Calibrated photos of the targets were taken in the field at a distance of approximately 1 m at 1:1 size reproduction using a Nikon D70 digital camera (Nikon Corporation, Tokyo, Japan). These were used to derive measures of target-background contrast at the immediate target boundary and with a broader area of bark around the target (both based on difference between the mean for the targets pixels and the mean of the pixels of the respective bark area); measures of visual 'clutter', both entropy and feature congestion, were also calculated. The computation of these metrics is described in the Supplementary Material. In non-technical terms, feature congestion estimates the amount of luminance and chromatic variation around the target, and orientation congestion the variation in the orientation of edges in the bark surrounding a target. Targets near rapid changes in luminance, chroma and edge-orientation are predicted to be harder to detect than targets further from such 'clutter'. The measure of sub-band entropy is based on different logic and, unlike feature congestion, is not based on any perceptual model. Instead it relates (inversely) to the amount of redundancy in an image and can be intuitively

156 understood in the same way as JPEG compression. A scene that is less cluttered
157 and more structured could be compressed more than one that has fewer similar
158 features within it.

159 Although all our targets were uniformly coloured, we also used the object recognition
160 measure applied by Stevens & Cuthill [27] in their analysis of disruptive camouflage.
161 This is because, as a result of the match between target and some immediately
162 adjacent bark areas being greater for some targets than others, the target edges
163 may be more detectable in some targets than others. Following Stevens & Cuthill
164 [27], a Laplacian-of-Gaussian edge detection algorithm was applied to the cropped
165 images containing the targets, and then coherent line-detection analysis was carried
166 out using the Hough transform. The Hough transform is a technique to estimate the
167 parameters of a shape from its boundary points within an image. It is the most
168 common method in Machine Vision for line detection. The number of straight lines
169 identified by the Hough transform in the correct location (i.e. on a target's true edge)
170 was used as the measure of success of 'triangle detection', so could take the integer
171 values from 0 to 3 [see 27 for additional information].

172 Relationships between the bird predation data (survival time, but measured at only 3
173 time points so not a continuous variable) and human detection data (binary
174 detect/miss and continuous detection distance) were analysed using non-parametric
175 correlation (Kendall's tau using the R function cor.test and the large sample size
176 normal approximation of the test statistic). Results for the human experiment, in
177 terms of the proportion of subjects detecting a given target, and the mean detection
178 distance were analysed using Generalized Linear Mixed Models with the R package
179 lme4 [30]. Binomial error was used for the detect/miss data and normal error for log-
180 transformed distance. For each predictor, two models were fitted using maximum

likelihood (both with participant as random intercepts), the first with the predictor in question, the second without the predictor, then these two models were compared using the change in deviance, for the binomial models tested against a chi-squared distribution or F test for the normal models [31]. Model assumptions (e.g. normality and homogeneity of variance), convergence and fit (residual deviance < degrees of freedom) were all validated, following [30, 31]. Because of the relatively large number of candidate predictors to be investigated, with concomitant risk of elevated type I errors and over-fitting, model selection ('training') and model evaluation ('testing') were carried out on different data [32]. This is a better approach than simply controlling type I error, because the outcome of any exploratory data analysis is best considered a 'hypothesis' to be tested with independent data. The 130 targets/cases were therefore randomly split into two sets of 65 using R's sample function. The first, training, set was used to build a model starting with all candidate predictors and then eliminating non-significant ($p > 0.05$) predictors in a stepwise fashion [31]. The candidate model was then tested using the other 65 cases. We present the results of the latter tests in the results section; the statistics associated with the training phase are provided in the Supplementary Material. Effect sizes are presented as odds ratios for the Cox regressions (bird experiment) or standardised regression coefficients (β, the change in the response variable for a change of 1 standard deviation in the predictor) for the GLMMs, both with 95% confidence intervals (abbreviated c.i.).

Results

Correlations between bird and human detection performance

In this analysis, if birds and humans find the same targets easy/hard to detect, we expect the correlation between the survival time under bird predation and the two human detection measures of detectability (proportion of, and distance, detected) to be negatively correlated (cryptic targets that survived longer under bird predation would be detected less often by humans and, if detected, at a shorter distance; i.e. closer to the tree on which they were placed). A modest negative association was indeed apparent for both probability of detection (τ = -0.18, z = -2.53, df =129, p = 0.0011) and distance (τ = -0.22, z = -3.27, df =129, p = 0.0115).

Analysing predictors of bird predation

Candidate predictors of detectability were the luminance and chromatic contrast between the target (a constant, as all were the same colour) and the surrounding bark at both its boundary and the broader tree background (so two contrast measures each at two spatial scales), measures of bark complexity based on three aspects of feature congestion (luminance, chroma and edge orientation) and sub-band entropy, plus the number of correct triangle edges detected by the Hough transform Orientation clutter and sub-band entropy were the only significant predictors left in the model training phase, but only orientation clutter was significant when tested on the independent data set (odds ratio = 0.62 (95% c.i. 0.48, 0.81), χ^2 = 10.4, df = 1, p=0.0013); mortality was lower on trees with more orientation clutter (Figure 1).

As mentioned before, if birds foraged more on some species than others, then the apparent effect of feature congestion could be an artefact of differences between tree species unrelated to bark texture. Certainly the species differed significantly in

bark complexity, with oak the highest on all metrics (Supplementary Material). However, in a series of models with both tree species and orientation congestion, and using all data (training and test) to maximise power, only orientation clutter was significant (Supplementary Material).

For comparison with Stevens & Cuthill [27], edge detection analysis was carried out using a Laplacian-of-Gaussian edge detector followed by the Hough transform as a straight line (and thus triangle outline) detector. Mortality was higher the greater the number of correct triangle sides detected by the Hough transform (odds ratio = 1.22 (95% c.i. 1.00 – 1.48), χ^2 = 3.88, df = 1, p = 0.0488). However, this edge salience measure had no significant predictive power in a model that included orientation clutter (lines: χ^2 = 2.10, df = 1, p = 0.1477; orientation: χ^2 = 10.99, df = 1, p = 0.0009).

Analysing predictors of human detection

All predictors using in the analysis of bird predation were also used in training models for both detection distance and probability of detection. However the calculations of these metrics were based on human, not bird, colour vision. For detection distance, orientation clutter and border luminance contrast were the only significant predictors left in the model training phase (Supplementary Material). Both were also significant when tested on the independent data: targets were detected at a greater distance when the luminance contrast at their border with the bark was higher (Figure 2; β = 0.10 (95% c.i. 0.02, 0.19), $F_{1,62}$ = 6.02, p = 0.0170) and orientation clutter was lower (Figure 2; β = -0.10 (95% c.i. -0.02, -0.19), $F_{1,62}$ = 5.69, p = 0.0201). For detection probability (0.84 of the prey were detected), the final

model in the training phase contained orientation clutter, chromatic contrast and Hough lines (Supplementary Material Table S4). However, when testing these predictors on the other 50% of the data, none were significant (orientation clutter: χ^2 = 1.77, p = 0.1832, chromatic contrast: χ^2 = 3.42, p = 0.0646, Hough lines: χ^2 = 0.85, p = 0.3565). However, it is worth noting that the non-significant patterns were consistent with those observed for detection distance (Supplementary Material).

Edge detection analysis was also carried out. Result shows that detection distance and detection probability were both higher the greater the number of correct triangle sides detected by the Hough transform (distance: β = 0.08 (95% c.i. 0.05, 0.11), $F_{1,128}$ = 6.55, p = 0.0117; detection probability: β = 0.08 (95% c.i. 0.05, 0.11), χ^2 = 18.183, df = 1, p < 0.0001;). However, for detection distance, this edge salience measure ceased to be significant when the significant predictors from the main analysis, orientation clutter and border luminance contrast, were included in the same model (single term deletions: Hough lines: $F_{1,126}$ = 0.16, p = 0.6920; orientation clutter: $F_{1,126}$ = 20.30, p < 0.0001; border luminance contrast: $F_{1,127}$ = 19.70, p < 0.0001). For detection probability, there were no significant predictors in the main analysis and so no formal justification for including these any possible alternative predictors for the relationship between detection probability and Hough lines. However, for interest's sake, if one fits the same model as for detection distance, the result is similar: Hough lines cease to be a significant predictor when orientation clutter and border luminance contrast are included in the same model (single term deletions: Hough lines: χ^2 = 1.68, df = 1, p = 0.1944; orientation clutter: χ^2 = 6.97, df = 1, p = 0.0083; border luminance contrast: χ^2 = 21.70, df = 1, p < 0.0001).

Discussion

The results show that it is more difficult to find objects against a complex background, and that detectability is both correlated between human and birds and explained by similar (although not identical) factors. Furthermore, we have demonstrated that we can quantify complexity in a meaningful way using metrics from computational vision. While previous studies on non-humans [e.g. 20, 21, 22] show that search time increases when searching against a complex background, or animals (killifish *Heterandria formosa*)[23] have a preference for hiding in visually heterogeneous habitats, these studies lack any quantification of "complexity"; analysis of what the features of any of the presumed distractors are that make search difficult, or whether the visual system codes different feature dimensions independently. In this experiment, we have shown that the application of metrics, particularly feature congestion, from machine vision, can provide insights to this question. It is perhaps notable that the more abstract, information-theory based, measure of "complexity", sub-band entropy, is not as good a predictor of search performance, in either birds or humans, as the metrics based on features in low-level vision [as shown also, previously, in humans by 26]. This would suggest that it is important for biologists to define what they mean by "complexity" of a background. Indeed, we prefer not to use that term for the effects observed in our study, preferring Rosenholtz's term of feature congestion (see also Endler's similar metrics [38]). It is not the general complexity of the visual scene that affects visual search, it is higher variance in some or all of the features of the object that is being sought. This parallels the conclusions Duncan & Humphreys [33] drew when reviewing the literature on human search for targets among discrete distractors, as opposed to the sort of continuous textures that bark, in our study, represents.

Our results also show that contrasts in luminance between target and background affect their detectability by humans negatively, i.e. as the similarity between target and the immediately adjacent bark decreases, the targets can be detected from further away. We had anticipated that this would be the main effect for both humans and birds in the experiment because the similarity in colour (luminance and chroma) of the targets to the background adds more noise in object segmentation at an early stage, facilitates the detection of boundaries [27] and makes feature grouping even more difficult [34, 35]. Indeed, considering the textures of targets and bark, as opposed to colour, the results we obtained are opposite to the predictions of background pattern matching: targets survived longer (birds) or are detected less easily (humans) on bark with greater levels of feature congestion, particularly oriented lines (edges). The targets, being a homogeneous colour, have a “feature congestion” of close to zero and so are most different from the backgrounds on which they are least detectable. Complexity of the background is more important than precise matching of the background in the situation studied: relatively simple targets and, at least in terms of pattern if not colour, complex backgrounds. We would expect this to reverse when targets are a very different colour from the background (e.g. bright white or yellow targets would stand out regardless of background complexity) or when backgrounds are simple and visually uncluttered.

Why was target-bark border contrast only significant for human detection distance and not for bird predation? While it is the case that the targets were designed to match the average bark as perceived by a bird, not a human, this is unlikely to be a major factor as luminance contrasts for bird and human measures were highly

correlated (Pearson r_{128} = 0.9937). One possible factor is lower sensitivity to luminance contrast differences in birds [36]. However, probably the main factor is that our measure of bird detection (predation checked at 24, 48 and 72 h) is less precise than the human measure, detection distance to the nearest 0.1 cm. Another factor is that human participants had one task – spotting triangles – whereas foraging birds were searching for multiple prey and had other behaviours competing for attention.

In both our bird and human experiments, the detectability of a target's edge, as measured by the Hough transform's performance, did predict target detection, but not independently of the contrast and congestion metrics. This is because the Hough transform is designed to detect linear edges of high contrast in luminance (or chroma), so edges in the background 'compete' with those on the triangular target's edges for the Hough transform's signal (if a straight line in the background is stronger than on the triangle's boundary, then the Hough transform will detect it preferentially). Therefore, the Hough transform's predictive success is completely specified by both target-bark boundary contrast and the number of strong edges in the background.

In summary, human and birds were shown to be affected by similar visual properties of the background when searching for cryptic targets. However, contrast between target and background seemed less important to birds on these backgrounds. That said, 'survival' is a crude measure compared to detection distance (as used for humans). Clutter metrics are related to saliency models of human vision, saliency being the attributes of an object that attract attention. Therefore, this approach also

offers an opportunity to understand the predictors of human and avian attention in the same framework, so that we can have further understanding of what components of visual scenes are important in driving visual search in different species.

Ethics statement

The human research had ethical approval from the University of Bristol, Faculty of Science Research Ethics Committee and the bird experiments from the Animal Welfare & Ethical Review Body.

Data accessibility

All data are available from Dryad doi: to be completed upon publication.

Authors' contributions statement

FX and ICC had equal roles in experimental design, execution, analysis and manuscript writing.

Competing interests

The authors declare no competing interests.

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Figure legends

Figure 1. Positive effect of bark orientation clutter on survival under bird predation. To plot the graph, orientation clutter was divided into four categories, from low to high, with approximately equal sample sizes in each [using the cut2 function in the Hmisc package in R, 37].

Figure 2. The distance at which targets were detected by humans was greater when orientation clutter was lower and luminance contrast between target and tree was higher. Distance is plotted on a log scale and so the lines represent linear regressions of log(distance) on the predictors.

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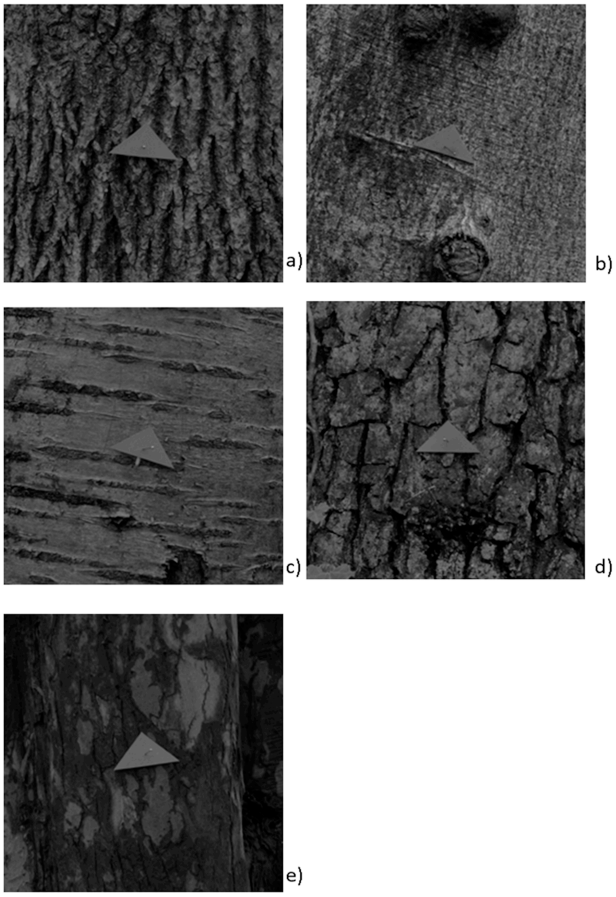

492

493 Figure 1

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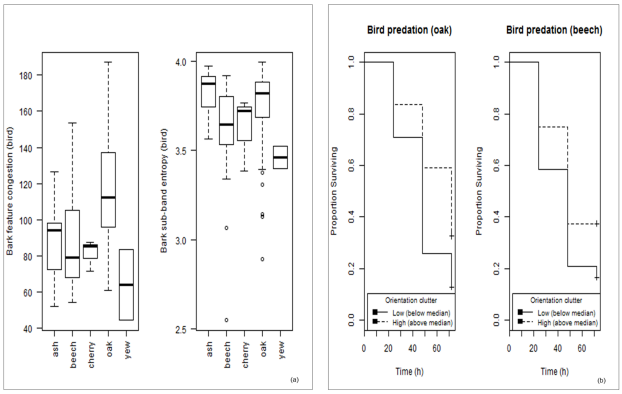
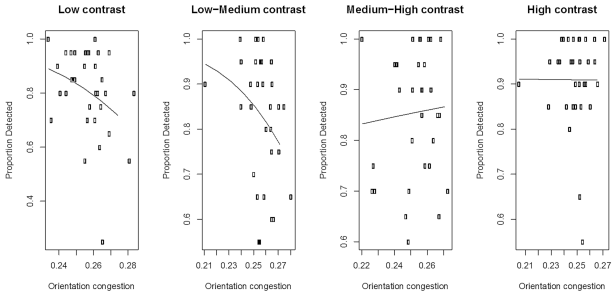

Bark feature congestion (bird)
Bark sub-band entropy (bird)
ash
beech
cherry
oak
yew
(a)
Bird predation (oak)
Bird predation (beech)
Proportion Surviving
Time (h)
Orientation clutter
Low (below median)
High (above median)
(b)

Figure 2

499



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501 Figure 3

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Supplementary Methods and Materials

The targets, being of fixed and known dimensions, were used to resize all images to a common scale (all images were downsized such that the analysed area – see figure 1 – was 256 x 256 pixels; thus image-processing time was not a limiting factor in analysis). Because digital cameras often show a non-linear relationship between the pixel value recorded and changes in light intensity, the images were first calibrated to linearize the RGB pixel values' relationship with light intensity [1]. A Gretag-Macbeth Mini-Colorchecker chart (X-Rite, Grand Rapids, Michigan, USA) was used as a colour standard in the images, allowing us to covert the camera's RGB values to linearized and device-independent sRGB. For human vision, the standardised sRGB values were then converted to L*a*b* colour space (CIELAB 1976; Commission Internationale de l'Eclairage; http://cie.co.at). CIELAB colour space represents colour in triplet coordinates of, first, lightness and, second, two of hue that approximate the red-green and yellow-blue opponent channels of humans [2]. It has the advantage that Euclidean distances in the colour space approximate perceived colour differences. This colour space is the result of decades of psychophysical experiments, modelling and arguments (it is still an approximation that does not hold under some conditions), so it is no surprise that there is no avian CIELAB. However, we constructed an equivalent colour space for a generalized passerine bird (these being the main avian predators of our targets), following the method of Stevens & Cuthill [3]. sRGB data were converted to photon catches of blue tit UV, S, M and L single cones, and double cones [4] using a standard D65 daylight illuminant [2]. D65 was used, rather than for example woodland shade [5] because, at the time and place of carrying out the experiment (winter), most targets

were illuminated by a mixture of skylight and direct sun rather than being in shade. The double cone photon catch was used as a surrogate for luminance (the L in L*a*b*); the ratio of (L – M) to (M + L) photon catch as a red-green opponent channel; the ratio of (M + L – 2*S) to (S + M + L) photon catch as a yellow-blue opponent channel. Each channel/dimension was scaled to lie between 0 and 1 (for L, black = 0 and 1 = white; for a, 0 = green, 1 = red; for b, 0 = blue, 1 = yellow). Luminance contrast was calculated as the distance in the L, or surrogate L dimension; chromatic contrast were calculated as the Euclidean distance in the 2D L*a*b*, or surrogate L*a*b*, chromatic space.

Luminance contrast of target against bark in both human and bird vision was calculated as the absolute difference between the target L value and the mean L of the bark at two spatial scales. First, within 2.5 target-widths of the target centroid, both horizontally and vertically. The image areas being analysed can therefore be visualised as a square of bark of sides that are 5 times the width of the target, with the target at its centre. Within that square, the contrast is between the mean for the target compared to the mean of the non-target (i.e. bark). The value 5 target-widths was chosen such that all images analysed included only targets and bark (not, for example, sky or other background features for narrow tree-trunks). Second, as a measure of the contrast between the target and the bark near the target's edge, a distance of one target-width from the target centroid: a square of bark that is 2 times with the width of the target, with the target at its centre. We call this 'boundary contrast' to distinguish it from the measures of local contrast that include a broader area of bark (5 target-widths). Chromatic contrast was analysed analogously, but as

552 the Euclidean distance calculated from the a and b (or pseudo-a and -b) colour
553 dimensions.
554
555 Complexity of the tree bark was calculated using two different clutter metrics: feature
556 congestion and sub-band entropy [6, 7]. The logic behind feature congestion is that
557 cluttered scenes are ones in which there are many features similar to features in the
558 target. The difficulty of detecting a target increases as background features that are
559 similar to the target's features increase in number. This parallels the effect of
560 distractors on performance in visual search tasks where the field of view contains
561 only discrete objects rather than a texture. In order to extract relevant information
562 from its surrounding, an animal needs information about rapid changes from one part
563 of the visual scene to another (which will relate to object boundaries, or that specify
564 the structure of objects). The scale of intensity change is determined by the range of
565 variation in the features processed in early vision. Thus the main measure of feature
566 congestion is rapid change in luminance, chroma and orientation of lines or "blobs"
567 (an edge detector responds to points as "short lines" of no particular orientation,
568 often called blobs in the computational vision literature). Both feature congestion and
569 sub-band entropy were calculated from the target-free 5-target-width squares used in
570 the contrast calculations, using the Matlab functions of Rosenholtz et al. [6, 7]. An
571 intuitive illustration of what the feature congestion metrics measure is provided in
572 figure S1; the application to experimental images is shown in figure S2). The
573 Rosenholtz et al. [6, 7] functions operate on a transformation of a calibrated RGB
574 photograph to L*a*b* colour space. Luminance and orientation clutter calculations
575 are based on the L dimension; chromatic clutter is based on the a and b dimensions.

Our equivalent for a bird instead passes image data in our avian surrogate L*a*b* colour space, as described above, to the Rosenholtz et al. [6, 7] functions.

All computations used the Image Processing Toolbox in Matlab [8] plus Rosenholtz et al.'s functions (available at http://hdl.handle.net/1721.1/37593). The latter also provide a weighted composite metric of feature congestion based on a weighted sum of luminance, chroma and orientation clutter. Because the weights are unknown for birds, we analysed the potential influence of the three feature congestion metrics separately for both taxa.

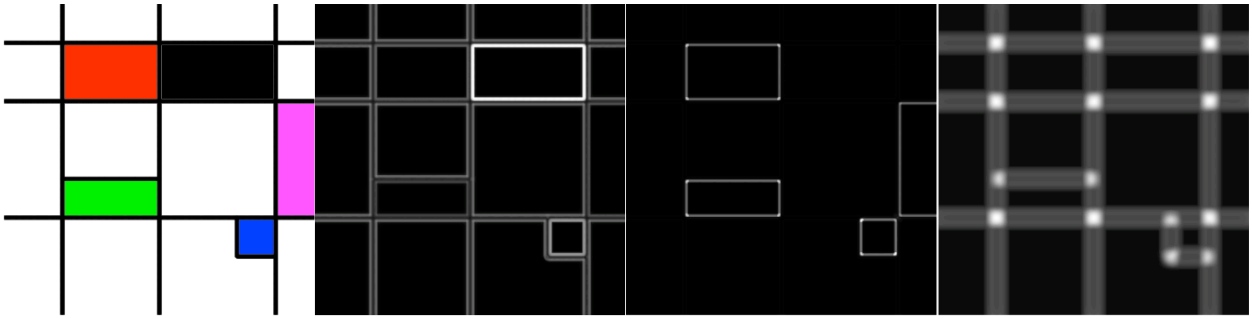

Figure S1 Intuitive illustration of the feature congestion metrics applied to a 'Mondrian' image. Left to right: (i) original 'Mondrian', (ii) the map of rapidly changing luminance, (iii) the map of rapidly changing colour, and (iv) the map of rapidly changing edge orientations.

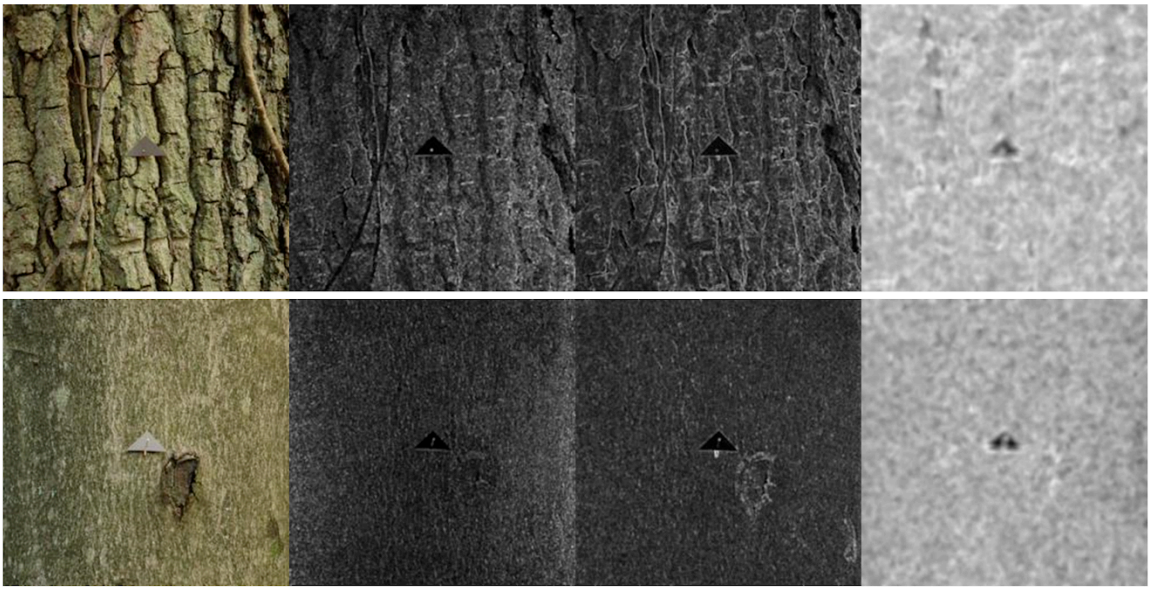

Figure S2 Examples of a target on oak bark (top row) and beech bark (bottom row), and feature congestion measures of complexity of the images. Top row (oak), left to right: (i) original image taken in the field, linearized and calibrated with human or bird vision model (here, human), (ii) luminance contrast image which is the map of rapidly changing luminance, (iii) chromatic contrast image which is the map of rapidly changing colour, and (iv) orientation congestion image which shows the map of rapidly changing edge orientations. In all cases, lighter areas represent regions of greater change. Bottom row is in the same sequence, but for a beech tree.

Supplementary Results

Bird predation

Using a randomly selected 50% of the cases, and starting with all nine predictors, step-wise backward elimination based on lack of statistical significance resulted in a final model with only orientation clutter and sub-band entropy (Table S1). When testing these predictors on the other 50% of the data, only orientation clutter was significant (orientation: χ^2= 10.4, df = 1, p=0.0013; sub-band entropy: χ^2= 0.41, df = 1, p = 0.5241). Mortality was lower on trees with more clutter in terms of oriented edges (odds ratio = 0.62; 95% c.i. 0.48 - 0.81).

Table S1. Model training: probability of avian predation.

Predictor	Step removed	χ^2	p
Border chromatic contrast	1	0.150	0.6981
Luminance contrast	2	1.019	0.3127
Border luminance contrast	3	0.414	0.5202
Chromatic clutter	4	0.949	0.3299
Luminance clutter	5	1.481	0.2236
Chromatic contrast	6	2.515	0.1128
Hough lines	7	3.324	0.0683
Orientation clutter	retained	8.082	0.0045
Sub-band entropy	retained	6.186	0.0129

All predictors had 1 df. χ^2 = likelihood ratio test from Cox regression. Chromatic contrast and Border chromatic contrast were log(1+x) transformed; sub-band entropy was log(4 - clut1se_wide) transformed.

The tree species differed significantly in bark complexity, with oak the highest (Table S2). However, in a model to predict prey survival using both tree species and orientation congestion, the former was not significant but the latter was (using all data to maximise power: tree species $\chi^2 = 4.54$, d.f. = 4, p = 0.3377; orientation $\chi^2 = 6.13$, d.f. = 1, p = 0.0133). As a more robust test, given the low sample size for some tree species, we repeated this analysing using only the two commonest in the sample, oak and beech (oak bark exemplifying complex bark, and beech with simple structure). Again, orientation congestion explained significant variation in survival when controlling for tree species ($\chi^2 = 9.70$, p = 0.0048) but tree species did not explain significant variation when controlling for orientation clutter ($\chi^2 = 0.004$, p = 0.9473). There was also no significant interaction between tree species and orientation clutter ($\chi^2 = 0.04$, d.f. = 1, p = 0.8437) and, although not significant for beech, the magnitude of the effect of orientation clutter was similar within each tree

628 species when analysed separately (oak: odds ratio = 0.73 (95% c.i. 0.57 – 0.95), χ^2
629 = 5.23, df = 1, p = 0.0222; beech: odds ratio = 0.72 (95% c.i. 0.49 – 1.05), χ^2 = 2.85,
630 df = 1, p = 0.0915).

631 **Table S2.** Variation in complexity of different tree barks

Variable	oak	ash	beech	yew	cherry	F	df	p
Luminance clutter	3.48 [a]	2.63	2.59 [b]	1.96	1.95	4.32	4,125	0.0026
Chromatic clutter	11.47 [a]	8.51 [b]	8.24 [b]	5.39 [b]	8.89	19.00	4,125	<0.0001
Orientation clutter	0.26 [a]	0.25 [b]	0.25 [b]	0.23 [b]	0.25	9.97	4,125	<0.0001
Sub-band entropy	3.76 [a]	3.82	3.60 [b]	3.46	3.62	4.58	4,125	0.0017

632 Values for each tree species are the means. Different letter superscripts indicate species means that
633 differ in pair-wise post hoc Tukey tests.

634 **Human detection**

635 Using the same randomly selected 50% of the cases as for the bird analysis, and
636 starting with all nine predictors, step-wise backward elimination was carried out for
637 detection distance (log-transformed, GLMM with normal error) and detection
638 probability (GLMM with binomial error). For detection distance the final model in the
639 training phase contained only orientation clutter and border luminance contrast
640 (Table S3). When testing these predictors on the other 50% of the data, both were
641 significant; targets were detected further away when border luminance contrast was
642 higher (β = 0.10 (95% c.i. 0.02, 0.19), $F_{1,62}$ = 6.02, p = 0.0170) and orientation clutter
643 was lower (β = -0.10 (95% c.i. -0.02, -0.19), $F_{1,62}$ = 5.69, p = 0.0201).

644 For detection probability, the final model in the training phase contained orientation
645 clutter, chromatic contrast and Hough lines (Table S4). When testing these
646 predictors on the other 50% of the data, in single term deletions from this full (three
647 predictor) model, none were significant (orientation clutter: χ^2 = 1.77, p = 0.1832,

chromatic contrast: χ^2 = 3.42, p = 0.0646, Hough lines: χ^2 = 0.85, p = 0.3565). Similarly, in step-wise backwards deletion none were significant (step 1, Hough lines: χ^2 = 0.85, p = 0.3565; step 2, orientation clutter: χ^2 = 1.30, p = 0.2544; step 3, chromatic contrast: χ^2 = 3.33, p = 0.0682). In the final model, the non-significant relationship with chromatic contrast was for detection probability to be higher when contrast was higher (β = 0.14 with 95% c.i. -0.01, 0.29). This was also true when using the full (130 case) dataset (β = 0.24 with 95% c.i. -0.14, 0.35; χ^2 = 19.01, p < 0.0001). In the penultimate model, the non-significant relationship with orientation clutter was negative: higher clutter was associated with lower detection probability (β = -0.09 with 95% c.i. -0.24, 0.07). Again, this was also true when using the full (130 case) dataset (β = -0.21 with 95% c.i. -0.33, -0.10; χ^2 = 13.54, p = 0.0002).

Table S3. Model training: human detection distance.

Predictor	Step removed	F	df	p
Chromatic clutter	1	0.13	1,55	0.7214
Sub-band entropy	2	0.69	1,56	0.4095
Chromatic contrast	3	0.30	1,57	0.5849
Luminance clutter	4	0.53	1,58	0.4688
Hough lines	5	1.22	1,59	0.2731
Luminance contrast	6	1.45	1,60	0.2331
Border chromatic contrast	7	1.86	1,61	0.1781
Border luminance contrast	retained	13.93	1,62	0.0004
Orientation clutter	retained	17.44	1,62	<0.0001

Chromatic contrast and Border chromatic contrast were log(1+x) transformed; sub-band entropy was log(4.9 - clut1se_wide) transformed.

Table S4. Model training: human detection probability.

Predictor	Step removed	χ^2	p
Luminance clutter	1	0.37	0.5419
Chromatic clutter	2	1.24	0.2655
Luminance contrast	3	2.63	0.1049
Border luminance contrast	4	2.05	0.1526
Sub-band entropy	5	3.42	0.0644
Border chromatic contrast	6	1.88	0.1701
Chromatic contrast	retained	4.99	0.0255
Hough lines	retained	18.4385	<0.0001
Orientation clutter	retained	10.92	0.0010

All predictors had 1 df. χ^2 = deviance change test. Chromatic contrast and Border chromatic contrast were log(1+x) transformed; sub-band entropy was log(4.9 - clut1se_wide) transformed.

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